Theses 2002 [Rob]

LINKED CHANGES IN PREY AVALIABILITY AND POPULATION STRUCTURE: USING ANTARCTIC FUR SEALS TO SAMPLE MARINE SYSTEMS

SARAH ROBINSON

DARWIN COLLEGE

UNIVERSITY OF CAMBRIDGE

Submitted for the M.Phil. Degree in Polar Studies

14th JUNE 2002

CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

This study tested hypotheses relating the foraging trip durations of lactating female Antarctic fur seals, to the abundance and availability of Antarctic krill, where the mean length of krill consumed is used a proxy of krill availability.

Over six years, 1568 foraging trips were measured for 178 individual seals, foraging from Bird Island, South Georgia. The relationships between the duration of these trips and the mean length of krill, derived from scat samples, was then investigated.

This study has shown large-scale changes in the krill population around South Georgia are easily detected in the foraging trip duration of female lactating Antarctic fur seals. The study found a positive correlation between foraging trip duration and the krill length, suggesting that longer trips, reflecting lower krill availability, are associated with a greater mean size of krill.

This study illustrates the important potential for predators, specifically female Antarctic fur seals, as samplers of a highly variable marine environment.

1. INTRODUCTION

1.1 General overview

Detecting and understanding the causes and consequences of long-term change in marine ecosystems is fundamental to many global concerns, not least to successful management of marine resources. Given the variation inherent in large marine ecosystems, even detection of systematic changes in physical process, such as climate warming, is very difficult. Only by understanding the natural variability of a marine ecosystem can the significance of long-term systematic changes, including those of potential anthropogenic origin, be assessed (Reid & Croxall 2001).

Finding ways to determine any patterns within the natural variability of the marine ecosystems is complex, as sampling it at scales appropriate to the process being measured is often logistically impossible. However it is important to investigate new ways of measuring ecosystem processes at appropriate scales in order to better understand the potential effects of long-term change associated with climate warming. It is the intention of this dissertation to analyse aspects of the marine ecosystem through an investigation of the population structure of Antarctic krill *Euphausia superba* (1.2) found in the scat samples of female Antarctic fur seals *Arctocephalus gazella* (1.3) on South Georgia (1.5).

1.2 Antarctic krill, *Euphausia superba*

In many marine ecosystems there are multiple prey species and a wealth of alternative pathways for the flow of energy/carbon from primary production to top predators. In the Antarctic there is a single dominant prey species, which forms a single link from primary producers to top predators. Antarctic krill *Euphausia superba* play a pivotal role in the ecology of the Southern Ocean. They are dominant primary consumers and constitute a crucial food source for many mammalian and avian predatory species (Brierley *et al* 1997). In a simplified Southern Ocean food web (Fig 1) it can be seen that krill are at the centre of a highly variable ecosystem that is dependent on them (Nichol & Mare 1993). *E. superba* is the single most important prey species taken by a range of higher predators (Croxall & Prince 1980, Reid *et al* 1996); a keystone species (Reid 2001).

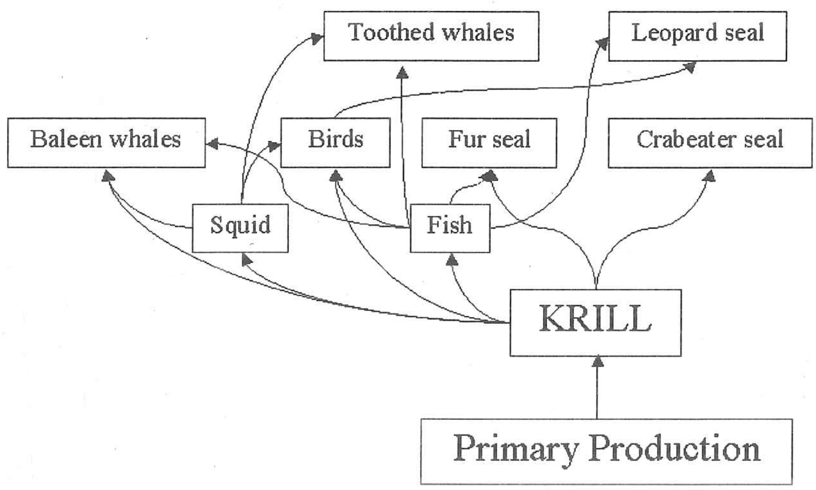

Figure 1. Simplified representation of Southern Ocean food web linkages that are centred around krill (Everson 2000).

There are 80 species of euphausiids widely distributed throughout the world's oceans (Everson 2000). The dominant species found in the Southern Ocean is *Euphausia superba* (Fig. 2) (Knox 1994). Due to the central position of krill within the Antarctic food web, and in more recent years to its commercial importance, the genus has been well studied. Because of the logistical and physical difficulties in sampling, however, little is understood concerning various aspects of this keystone species.

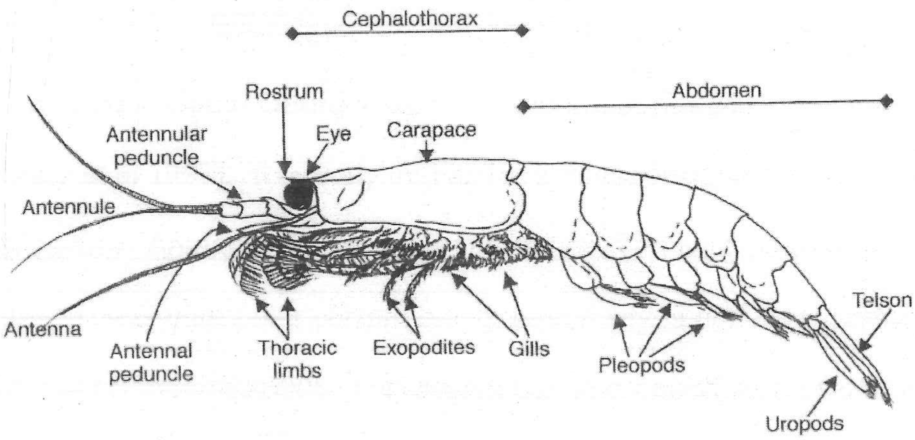

Figure 2. Generalised view of a euphausiid showing the main morphological features relevant to identification (Everson 2000).

Krill are usually found in dense aggregations which can be classified as patches, shoals, swarms or schools according to the density of individuals and the physical characteristics of the aggregation, the composition of the aggregation is variable in terms of sex, maturity and length (Watkins *et al* 1992). The swarming behaviour of Antarctic krill is a feature of its biology, the density and distribution of these aggregations making this species of particular interest both scientifically and commercially (Watkins *et al* 1992).

Despite their importance in the ecosystem there is a major limitation with regard to the age of krill. Currently krill are aged on the basis of length; hence attempts to study the population dynamics of krill are dependent upon measurements of krill length in order to construct length-of/at-age distributions to examine population structure.

The waters around South Georgia are known to support high concentrations of krill (Brierley *et al* 1997). It is likely that krill are transported into the South Georgia region in Antarctic Circumpolar Current or Weddell Sea water (Watkins *et al* 1999). The circum polar current being, effectively, a conveyer belt on which krill are carried (Everson 2000). The distribution and abundance of krill in the South Georgia area are dependent on a number of oceanographic and biological characteristics and events operating both in the immediate vicinity of South Georgia and on a larger scale in the highly productive Scotia Sea and beyond (Reid & Arnould 1996, Croxall *et al* 1985).

As the Antarctic circumpolar wave rotates around the continent with a 4 to 5 year periodicity, the extent of the sea ice cover in the southern ocean has been shown to oscillate regionally (Murphy *et al* 1995). Extended sea ice cover and large spatial extent during winter is favourable for an early onset of the spawning season (Everson 2000). This is probably due to the ice algae resource available to krill during late winter to early spring, krill having been frequently observed feeding in pressure zones, melting ice and infiltration layers where ice provided both confining crevices and rich algal growth (Bergstrom *et al* 1989). It is possible that the crevices also provide protection from predation resulting in a higher survival rate, which is further increased by a severe winter. Moreover, the environment beneath winter sea ice seems to provide a favourable habitat for larval krill development (Everson 2000). If krill at South Georgia have their origins in the peninsular region, then seasons characterised by increased ice cover there could propagate high krill abundance around South Georgia and other downstream locations (McCafferty *et al* 1998, Brierley 1997).

Estimation of the standing stock of *E. superba* presents enormous logistical difficulties, not least because its distribution extends over much of the 36 million square kilometres, which make up the Southern Ocean (Everson 2000). The problems are exacerbated by the fact that a significant part of this area is covered by sea-ice. As a result of these difficulties, there is a lack of adequate within- and between-year sampling of krill populations, even on a small scale (Murphy & Reid 2001). However Reid *et al* (1999) show the possibility of using marine predators as effective samplers of krill populations and the Antarctic fur seal is especially suited to use as a system sampler.

1.3 Antarctic fur seals *Arctocephalus gazella*

Like all seals, sea lions and walrus, Antarctic fur seals *Arctocephalus gazella*, belong to Pinnipedia, which has three families. The family Otariidae, whose members are known as eared seals, is divided into two groups, sea lions and fur seals (Bonner 1994). All otariids are polygynous, gregarious and sexually dimorphic in body size (Gentry & Kooyman 1986). There are nine species of fur seal comprising of two genera, *Arctocephalus* and *Callorhinus*. *Callorhinus* have only one species, the northern fur seal, and of the eight remaining genera only one is not found in the Southern Hemisphere so *Arctocephalus* are often referred to as the southern fur seal (Bonner 1994). Southern fur seals have a grizzled appearance, generally coloured dark grey brown on the back, shading lighter beneath. Pups are born with a black or very dark brown natan coat, through which white-tipped hairs gradually grow, one or two thousand pups per year are born with white coats (Bonner 1994).

Antarctic fur seals adult males can obtain a maximum mass of 150 to 200 kg, with a mean mass of 130kg, up to five times that of the female (Payne 1979). The nose-to-tail lengths also demonstrate the sexual dimorphism, males reaching 165-200 cm and females 115-140cm. The population is estimated at more than three million individuals and is currently increasing (Boyd 1993).

Over 95% of the Antarctic fur seal population breeds at the island of South Georgia (Doidge *et al* 1986). The strongly seasonal environment imposes a stringent pattern on its breeding. Females become sexually mature at age three years, bulls take longer to mature, but grow faster, attaining breeding status between the ages of 7 and 10 (Bonner 1994). Because of the intense polygyny of these seals, however, many bulls may never mate (Bonner 1994). The breeding season begins with the arrival of the bulls in late October, territories being established with displays and fighting. The first cows arrive into the territories from the sea in the second week of November. The number of cows per territory is highly variable but averages between 11 and 16 (Bonner 1994). Pupping extends from late November to late December, with the median pupping date in the range 4-8 December. Adult females haul-out, give birth two days later, and then remain ashore with there pups for approximately seven days, during the perinatal attendance period (McCann & Doidge 1987). At the end of this period, the female comes into oestrus and mates with the bull in whose territory she is (Bonner 1994).

Like all lactating otariid seals (Pinnipedia: otariidae), Antarctic fur seal females alternate between short nursing periods ashore and regular foraging trips to sea (Arnould & Boyd 1995, Boyd 1999). During pup rearing, females feed almost exclusively on Antarctic krill (Croxall & Pilcher 1984, Doidge & Croxall 1989, Costa *et* al 1989). Lactation lasts 112 days (range 90-126) during which the female makes approximately 16 trips to sea (range 12-21) (McCann & Doidge 1987). The season of attendance lasts until April when weaning occurs (Doidge *et al* 1986).

Throughout the season of attendance, maternal foraging trip duration (foraging trip duration) increases, as the age, suckling ability and stomach capacity of the young develops (Arnould *et al* 2001). Like other animals provisioning their offspring from a remote food source, Antarctic fur seals face a number of decisions: how long to search before returning to offspring, how much food to provide for offspring and how long to stay with offspring (Arnould *et al* 2001). In the specific case of marine predators, parental foraging time budgets appear to vary in relation to the resources available (Arnould *et al* 2001). During periods of relative food shortage the foraging trip duration increases (Boyd 1999). The Antarctic fur seals diet consists predominantly of Antarctic krill, which they appear to capture mostly at night. Adult male fur seals take a higher proportion of fish and squid prey compared to the krill-dominated diet of the female, whose diet consists of more than 90% krill (Bonner 1994). The pattern of dive lengths and depths corresponds with the vertical migration of krill, ensuring that the seals obtain their food in the most economical way, avoiding deep dives, which are energetically more costly than shallow ones (Bonner 1994).

1.4 Using predators as samplers.

During the breeding season, female Antarctic fur seals alternate between periods of foraging at sea and time ashore suckling their pups. As a result of these restrictions they can be considered central place foragers during the summer months. This strategy means they are particularly suited to use as system samplers. Krill collected from their faeces can provide detailed information on changes in the population structure of krill at a temporal scale (Reid 2001).

Because changes in krill population dynamics and accompanying fluctuations are essentially unknown, predators may potentially have a key role to play as indicators of environmental variation in the Southern Ocean at a range of spatial scales, which cannot be exploited using conventional sampling methods (Reid *et al* 1999). Recent work shows that krill in the diet of predators, in particular Antarctic fur seals at South Georgia, provided a reliable and consistent representation of the structure of the krill population (Reid *et al* 1996).

One advantage of predator sampling is that it is possible to collect data over longer temporal scales than may be possible in a ship-based sampling programme (Everson 2000). Reid *et al* (1999) showed that there is good correspondence between the combined size distribution of *Euphausia superba* taken by several different predator species (Macaroni penguins and Antarctic fur seals) and the size distribution derived from a series of net hauls conducted in the same area at the same time.

1.5 South Georgia and CCAMLAR

South Georgia lies between latitudes 53° 56' and 54 ° 55' S and longitudes 34 ° 45' and 38 ° 15' W. It is an isolated sub-Antarctic island in the Southern or Antarctic Ocean. Its location close to the Antarctic convergence (Antarctic Polar Frontal Zone), combined with the Antarctic circumpolar current, has resulted in a region characterised by high biomass and productivity of phytoplankton, zooplankton and vertebrate predators (Atkinson *et al* 2001). The commercial exploitation of South Georgia's abundant wildlife was quick to follow Captain Cook's reports, published after his exploration of the island in 1775. As virtually no attempt was made to conserve the stocks by sealers or government, the sealing operations resulted in the near extinction, first of several species of seal, and eventually the industry itself (Headland 1984). However, the Antarctic fur seal population is now estimated at more than three million; a large proportion being found on South Georgia (Boyd 1993). The recovery of the fur seal populations from near extinction is remarkable testimony to the resiliency of animals to the effects of such exploitation.

Today, measures are in place to safeguard the environment and to prevent such exploitations reoccurring by protecting the integrity of the ecosystem of the seas surrounding Antarctica. Within the Antarctic Treaty System the convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) is in place for the protection and preservation of the Antarctic environment. The concentration of marine living resources found in Antarctic waters, and the increased interest in the possibilities offered by the utilization of these resources as a source of protein, has amplified the urgency to increase knowledge of the marine ecosystem and its components (Laws 1993).

Decisions on harvesting need to be based on sound scientific information. In the case of krill regular, direct, and representative samples of population are difficult to obtain. Logistically, it is incredibly difficult to sample the Southern Ocean population of krill and make concurrent estimates of population structure and biomass. The lack of adequate within- and between-year sampling of population structure has meant that it has been difficult to distinguish changes within the population from gross changes in overall abundance (Murphy & Reid 2001). The use of predators as samplers enables regular samples of the krill population to be obtained.

1.6 Aims

This project will examine concurrent changes in the Antarctic fur seal foraging trip durations and the population structure of Antarctic krill during the pup-rearing periods of 1996-2001. In effect, the predator will be used to provide information about the changes in prey, rather than the predator itself. This will include important data on krill size and population structure, as well as on the availability prey in the course of foraging.

To achieve this, the project will use data on the foraging trip duration of Antarctic fur seals in a novel way in order to examine relatively short-term changes in the availability of Antarctic krill. Distinct changes in the population structure of krill have been implicated in the large-scale variability in krill abundance observed at South Georgia. This project will examine the role of changes in krill population structure in an attempt to determine what drives the changes in the abundance. This will allow data to be collected at time-scales that are simply not available using ship-based sampling. While it is likely that the variable nature of the marine ecosystem in this area will mean that finding clear and consistent patterns during the course of a single year may be difficult, it is possible that using a multi-year data set, a set of general patterns may be detected.

Aim: To determine whether changes in the duration of foraging trips undertaken by lactating female Antarctic fur seals provide a proxy for relative krill abundance and can be linked to concurrent changes in the population structure of krill as observed in the Antarctic fur seal diet.

2. METHOD

2.1 Data Collection

All data were collected on Bird Island, South Georgia (54°00′ S, 38°02′ W) as part of the British Antarctic Survey programme examining the role of marine predators in the Antarctic marine ecosystem. The foraging trip duration (ftd) for between 20 and 40 lactating female Antarctic fur seals were recorded for each year from 1996-2001 during the pup-rearing period (December to March). Each study animal had a small VHF transmitter glued to the fur on the mid-dorsal region during the peri-natal period in order to measure the duration of the subsequent foraging trips. Each transmitter emits a pulsed signal at 1-second intervals at separate frequencies. The signals were logged using a remote receiver that scans through the range of frequencies and records and stores all signals detected. Over the same time periods, weekly samples of krill carapaces were collected from Antarctic fur seal scats. Reid and Arnould (1996) have described a reliable method of faeces analysis widely used by other researchers. Up to 10 scats are collected each week between late December and early January. Each scat is individually bagged and, where immediate processing is not possible, stored frozen (-20°C). Collection of scats is concentrated in areas used predominately by lactating female seals and care is taken only to collect whole fresh scats. By suspending the scat in a solution of detergent (1%) and disinfectant (1%) in a glass beaker, the scat is gently disintegrated. The differential settling rates of components allowing denser objects to settle out. The supernatant fluid is then decanted into a sorting tray and the beaker topped up with solution. The process of gentle agitation, partial decanting and re-suspension is continued until no further remains passed over into the sorting tray. The residue in the beaker is then sorted under a binocular microscope (x6).

2.2 Data Processing

Although the recording of the VHF signals is automated, the estimation of foraging trip duration requires visual inspection of the data due to a combination of radio interference and the behaviour of the animals while ashore (Reid *personal communication* 2002).

The data from the remote receiver is conveniently represented by charts that show signal strength as a function of time as shown in Figure 3. There are periods with relatively 'low' signals interspersed by periods with 'high' signals. The blocks of high signal strengths represent periods ashore, when the transmitter signal was recorded. The low levels represent interference during foraging periods. The foraging trip duration for each trip was analysed using purpose written software in Matlab (www.mathworks.co.uk), which produced an output of the number, duration and date of foraging trips for each seal.

Measurements of the carapace lengths of krill found in samples were used to determine krill length in the diet of Antarctic fur seals. Frequency distributions of krill length over time provide an indication of changes in the prey population structure. The krill total length was estimated from the removed carapace length and width measurements following the method of Reid and Measures (1998).

2.3 Data analysis

The analysis began with a series of graphical representations of both the ftd and krill length to examine any patterns in the data. The data was first manipulated to determine the most illuminating way for it to be represented and statistically analysed.

Initial statistical analysis examined inter-annual variability using the raw data. 1-way analysis of variance (ANOVA) was used to determine if any difference between the years could be found. A correlation between mean ftd and mean krill length was then tested. To observe intra-annual variation each year was divided into 14-day periods with the first time period beginning on the first of November for each year. In looking for relationships within each year between ftd and date and between krill length and date, regression analysis was used. Finally ftd and krill length were correlated for each year and then the for time periods 3-5 for all years. Statistical values are considered significant if they have a probability value (*P* value) above the 95% confidence limit.

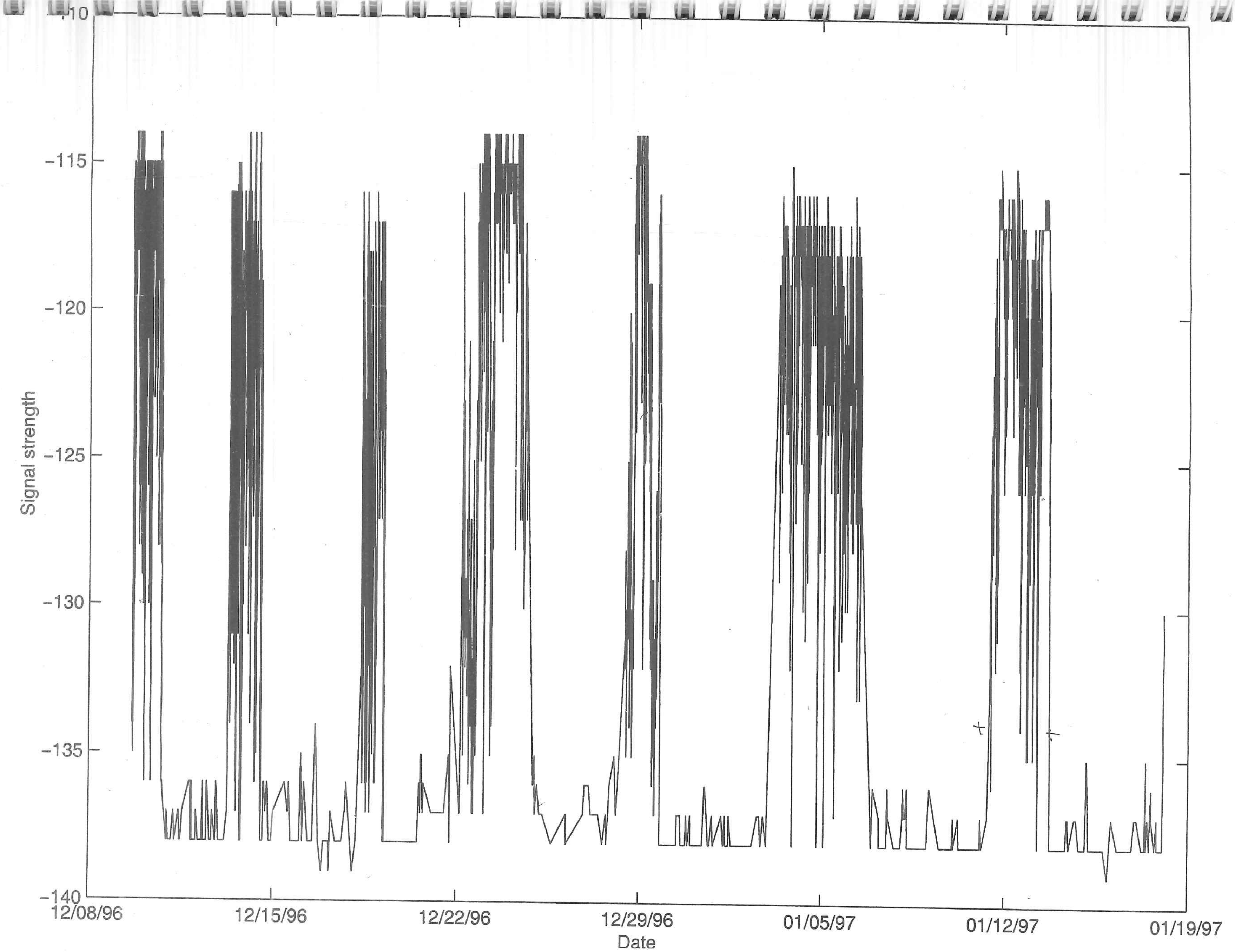

Figure 3. An example plot from 1997, showing signal strength as a function of time.

3. **RESULTS**

3.1 INTER-ANNUAL VARIABILITY

3.1.1 Foraging Trip Duration (ftd)

H^o = There is no significant difference in the foraging trip duration between years

Over 6 years of data 178 seals were tracked over a total of 1568 foraging trips (Table 1). There was a significant difference in the foraging trip duration between years (1 way-ANOVA $F_{(1,5)} = 12.15$ $P < 0.001$), the greatest difference being seen between 1996 and 1998 (Figure 4).

Table 1: The totals for each year, the time periods corresponding to fourteen-day periods, time period one beginning on the first of November for each year.

Year	n_{seals}	n_{ftd}	$n_{time\ periods}$
1996	32	410	8
1997	28	235	9
1998	31	213	8
1999	28	298	9
2000	35	255	7
2001	24	196	6

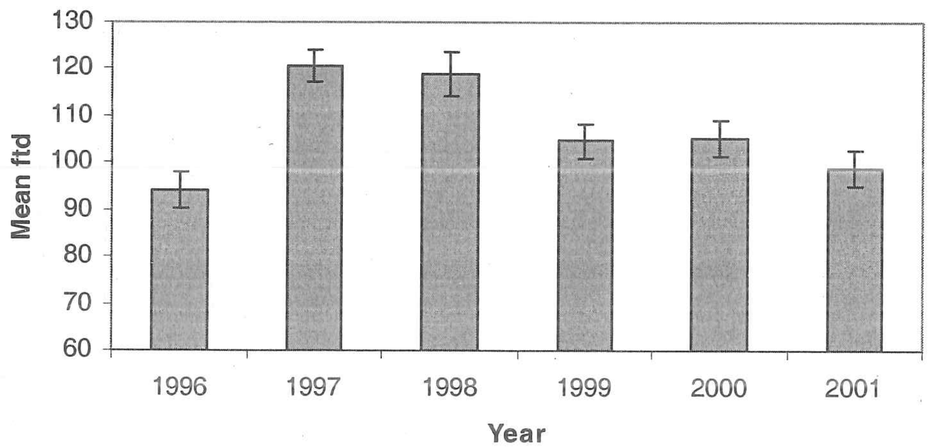

Figure 4: The mean (± Standard Error, SE) foraging trip duration for each year

3.1.2 Krill population structure

H^o = There is no significant difference in krill length between years

A total of 9010 krill lengths were measured over the course of 6 years and there was a significant difference in the mean size between years (1 way-ANOVA $F_{(1,5)}$ = 473.84 $P< 0.001$)(Table 2). The greatest differences in krill population structure were seen between 1996 and 1999, with evidence of bimodality in 1998.

Table 2: The totals for each year, the time periods corresponding to fourteen-day periods, time period one beginning on the first of November for each year.

Year	n krill length measurements	n time periods
1996	1565	7
1997	1439	5
1998	1686	8
1999	1463	8
2000	1191	6
2001	1666	6

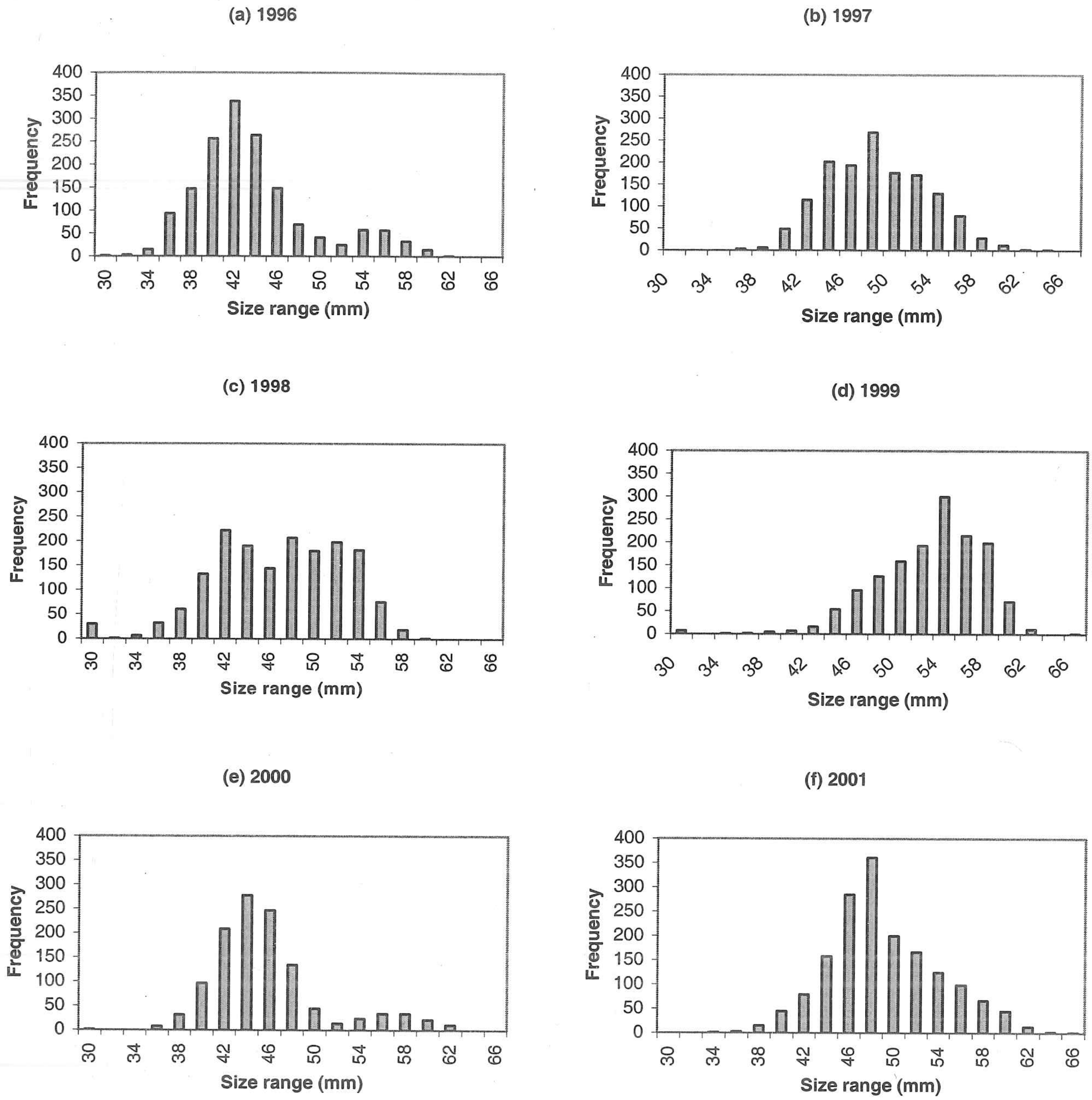

Figure 5: Annual krill length frequency distributions, for years: (a) 1996, (b) 1997, (c) 1998, (d) 1999, (e) 2000 and (f) 2001.

3.1.3 Foraging trip duration and krill population structure

H^o = There is no significant correlation between foraging trip duration and krill length

Although both foraging trip duration and mean krill length varied between years there was no correlation between mean foraging trip duration and mean krill length ($r = 0.239$ $P = 0.648$)

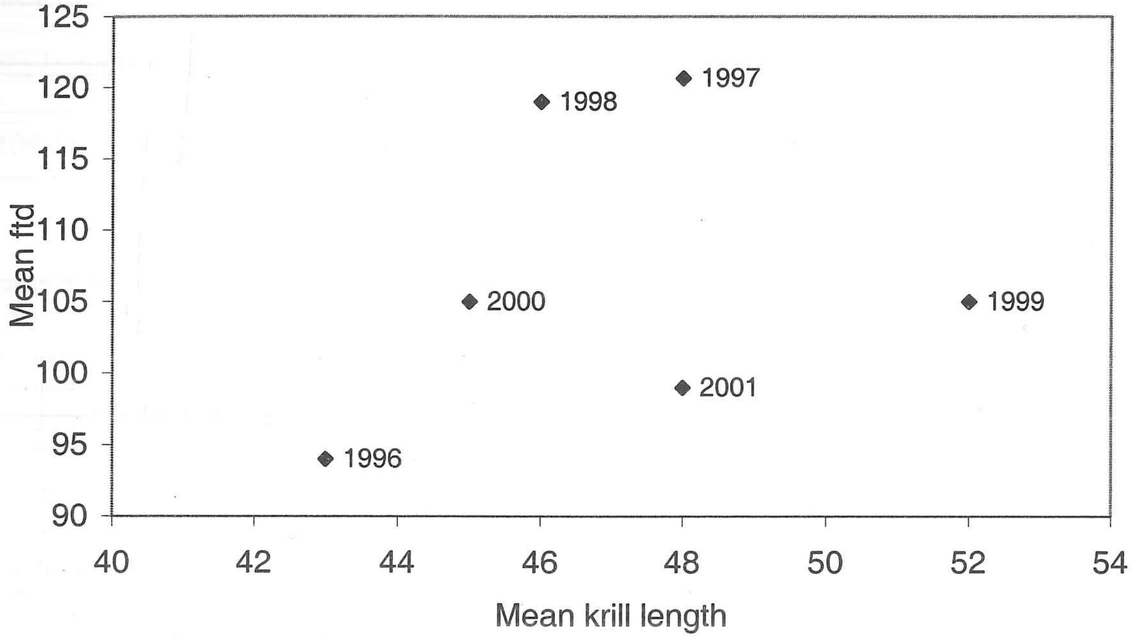

Figure 6: Plot showing mean foraging trip duration and mean krill length, 1996 -2001

3.2 INTRA-ANNUAL VARIATION

3.2.1 Foraging trip duration

H^{o} = There is no significant difference between foraging trip duration and time

There is substantial variation in the foraging trip duration during within each year (fig 7), with a significant increase in foraging trip duration during all years with the exception of 1998 (Table 3). In order to consider the pattern of change within each year the mean foraging trip duration for each 14-day period was calculated (fig 7); this indicated that in four out of six years there was a general period of stability in time periods 3-5 and an increase there after, again with the exception of 1998.

Table 3: Relationship between foraging trip duration and days after November 1 (days) from1996 to 2001 (sample sizes given in table 1).

Year	Equation	*F*	P
1996	96 ftd = 45.9 + 0.605 n days	77.21	<0.001
1997	97 ftd = 62.4 + 0.799 n days	29.50	<0.001
1998	98 ftd = 98.7 + 0.246 n days	2.83	0.094
1999	99 ftd = 79.4 + 0.306 n days	13.70	<0.001
2000	2000 ftd = 59.6 + 0.677 n days	42.23	<0.001
2001	2001 ftd = 62.8 + 0.516 n days	14.50	<0.001

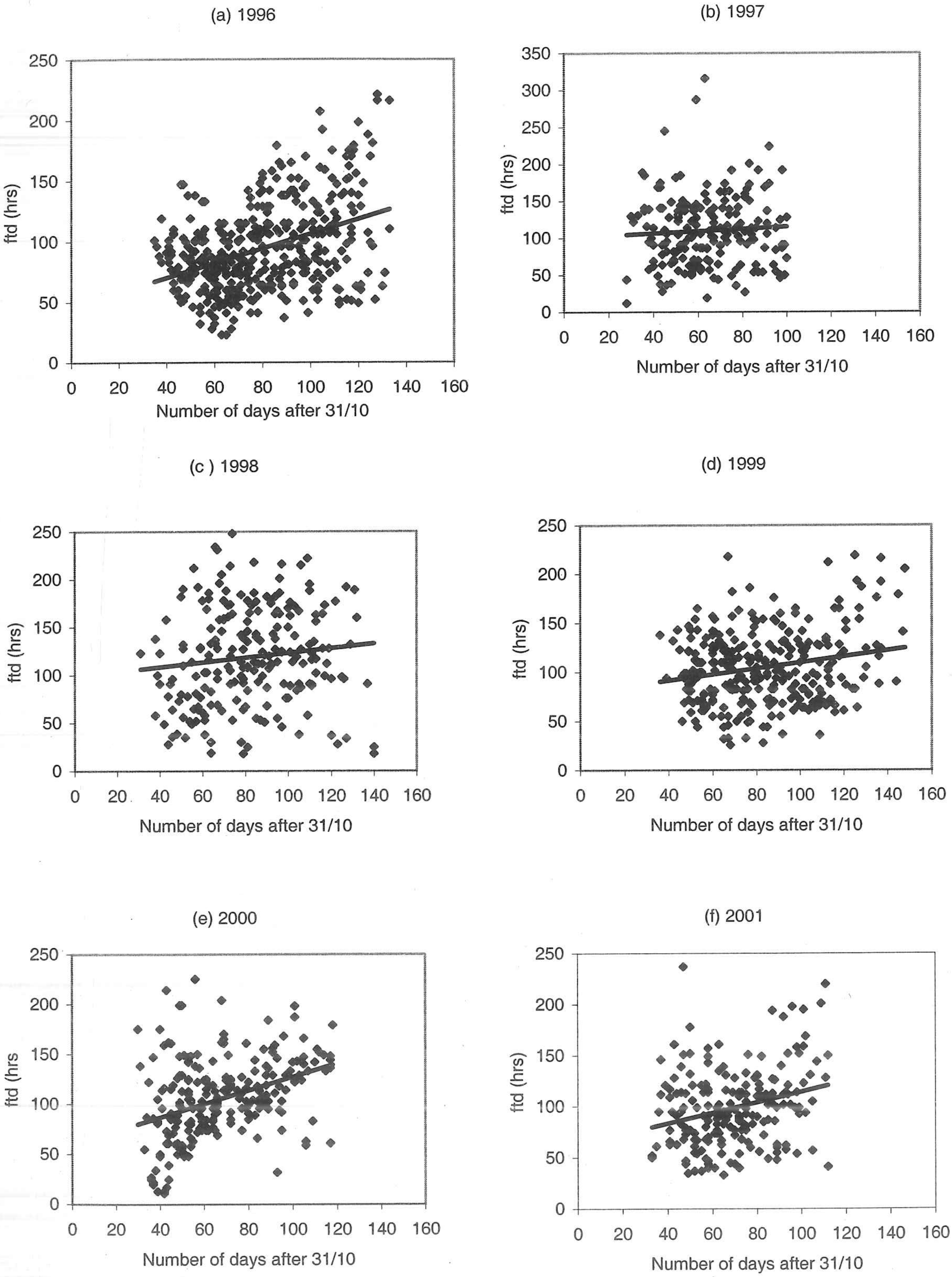

Figure 7: The distribution of foraging trip durations throughout the lactation period (December to March) for each year (a. 1996, b. 1997, c.1998, d.1999, e.2000 and f. 2001).

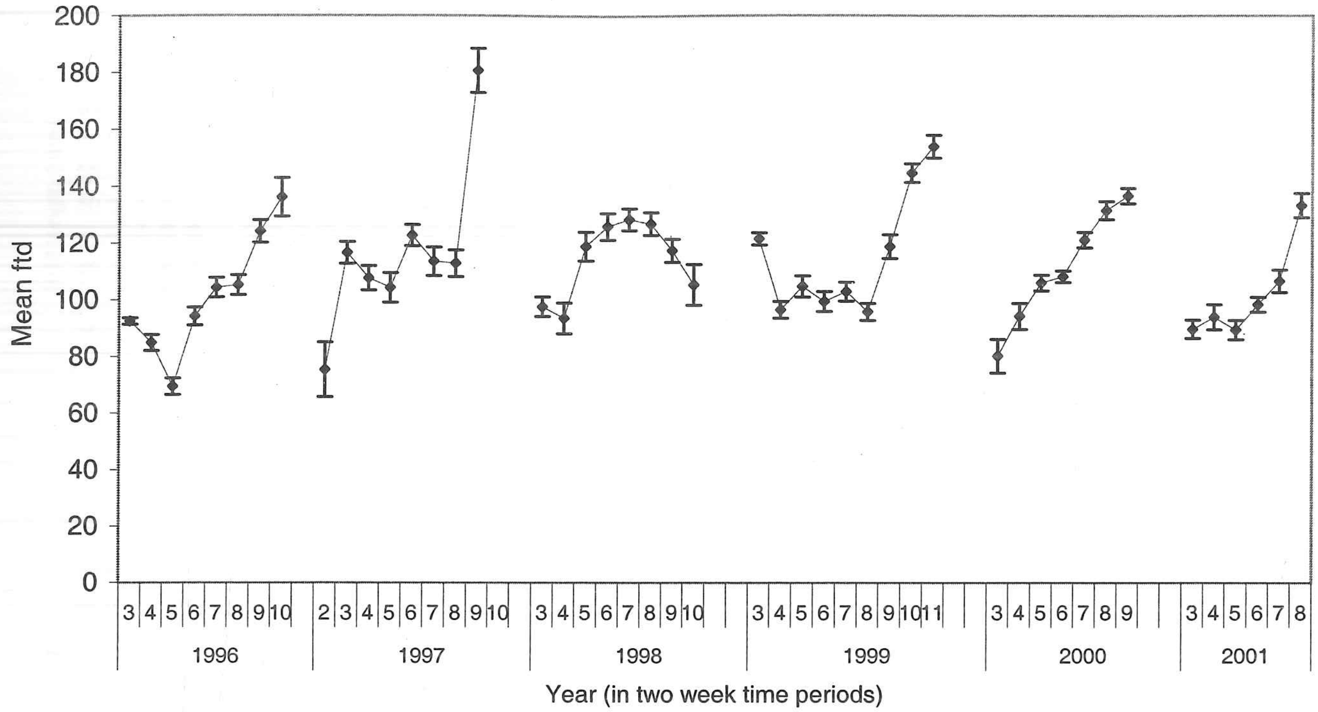

Figure 8: Mean foraging trip duration (± SE) for two-week periods 1996-2001 (see methods for details on time period calculation 2.3).

3.2.2 Krill population structure

H° = There is no significant difference between krill length and time

There was significant decrease in the size of krill in each year with the exception of 1996 and 1999, however the positive relationship was only significant in 1996 (Fig 9, Table 4). In order to consider the pattern of change within each year the mean krill length for each 14-day period was calculated (fig 10).

Table 4: Relationship between krill length and days after November 1 (days) from1996 to 2001 (sample sizes given in table 2).

Year	Equation	*F*	P
1996	Mean length = 39.8 + 0.0300 day	31.65	<0.001
1997	Mean length = 50.1 - 0.0272 day	39.14	<0.001
1998	Mean length = 47.7 - 0.0272 day	41.39	<0.001
1999	Mean length = 51.0 + 0.00740 day	2.74	0.098
2000	Mean length = 47.8 - 0.0267 day	45.59	<0.001
2001	Mean length = 48.9 - 0.00900 day	9.71	0.002

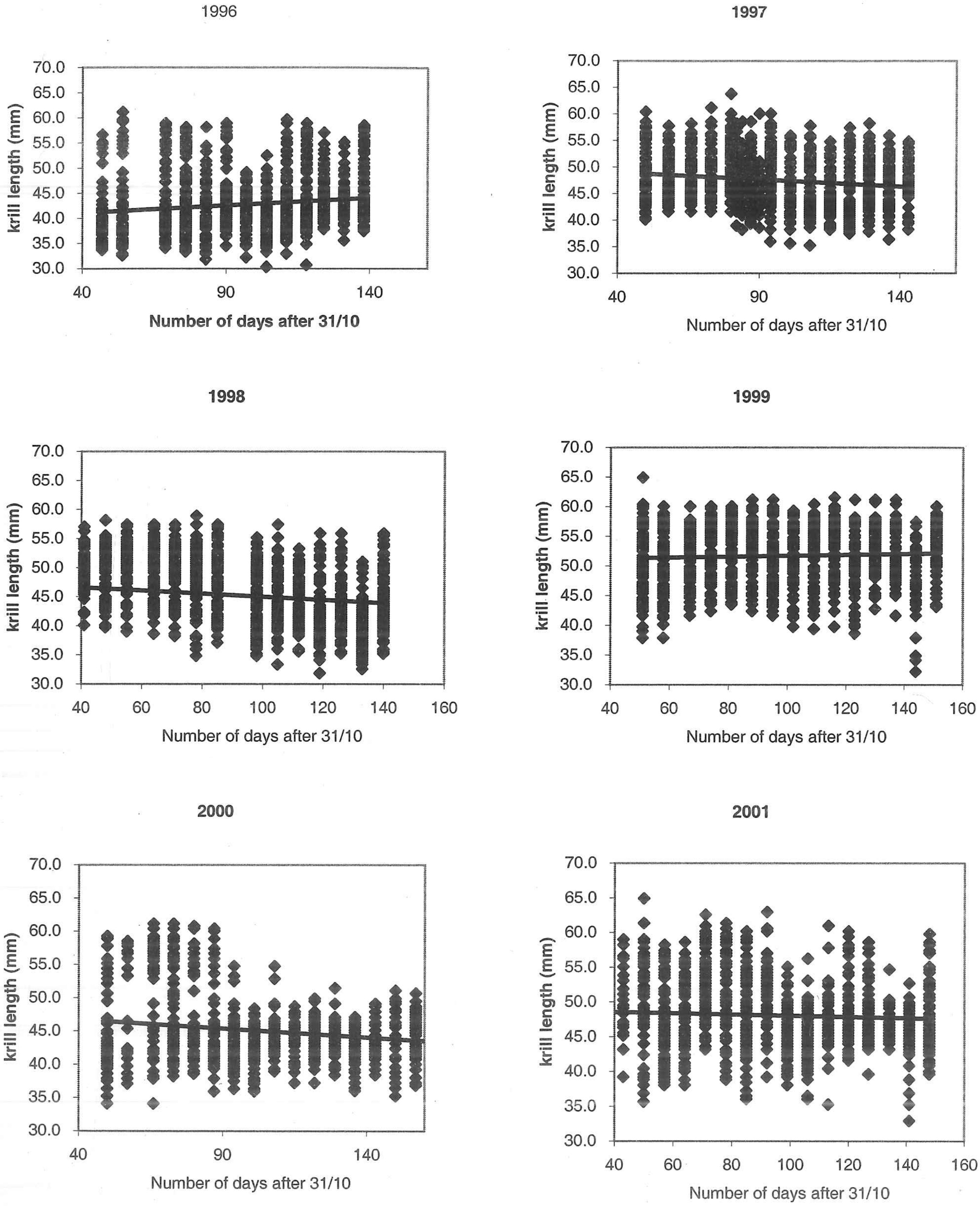

Figure 9: The distribution of krill lengths from fur seal scat samples collected throughout the lactation period (December to March) for each year (a. 1996, b. 1997, c.1998, d.1999, e.2000 and f. 2001).

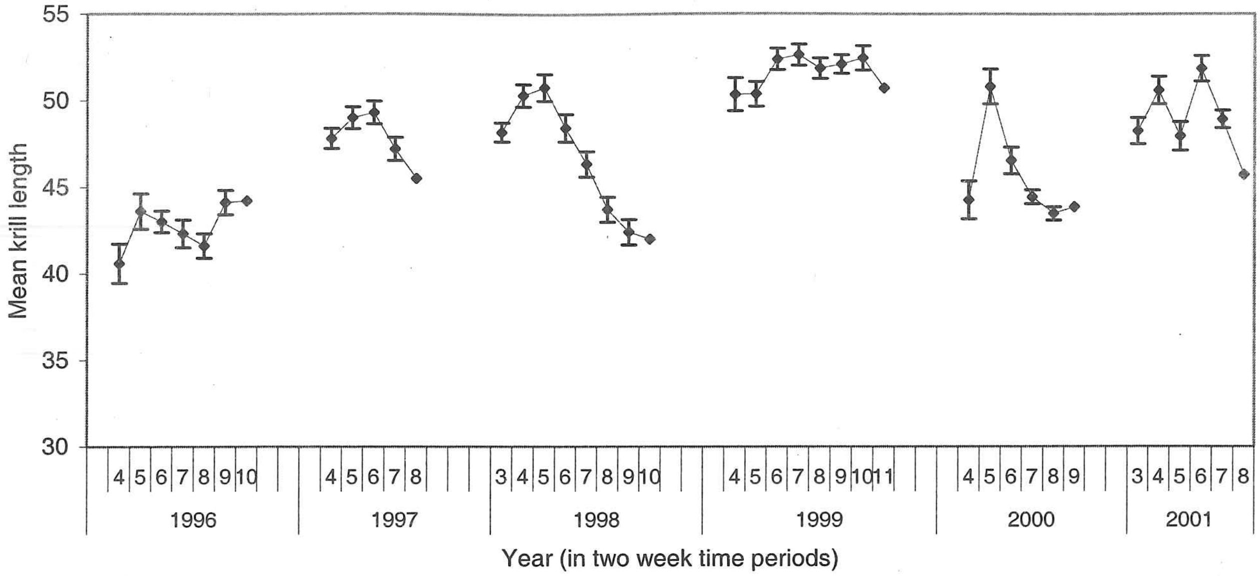

Figure 10: Mean krill length (± SE) for two-week periods 1996-2001 (see methods for details on time period calculation).

3.2.3 foraging trip duration and krill population structure

Despite the temporal changes within years there was no correlation between foraging trip duration and krill length in any year (Table 6). Similarly when all data were pooled across years there was no correlation ($r = 0.239$, $P = 0.648$) (Fig 3), however when the analysis was restricted to the foraging trip duration and krill lengths for time periods 3 to 5 there was a significant relationship ($r = 0.644$, $P = 0.013$)(Fig. 8).

Table 5: Correlation of the mean foraging trip duration and mean krill length for each year

Year	r	P value
1996	0.446	0.316
1997	-0.422	0.258
1998	-0.226	0.591
1999	-0.008	0.985
2000	-0.463	0.355
2001	-0.579	0.229

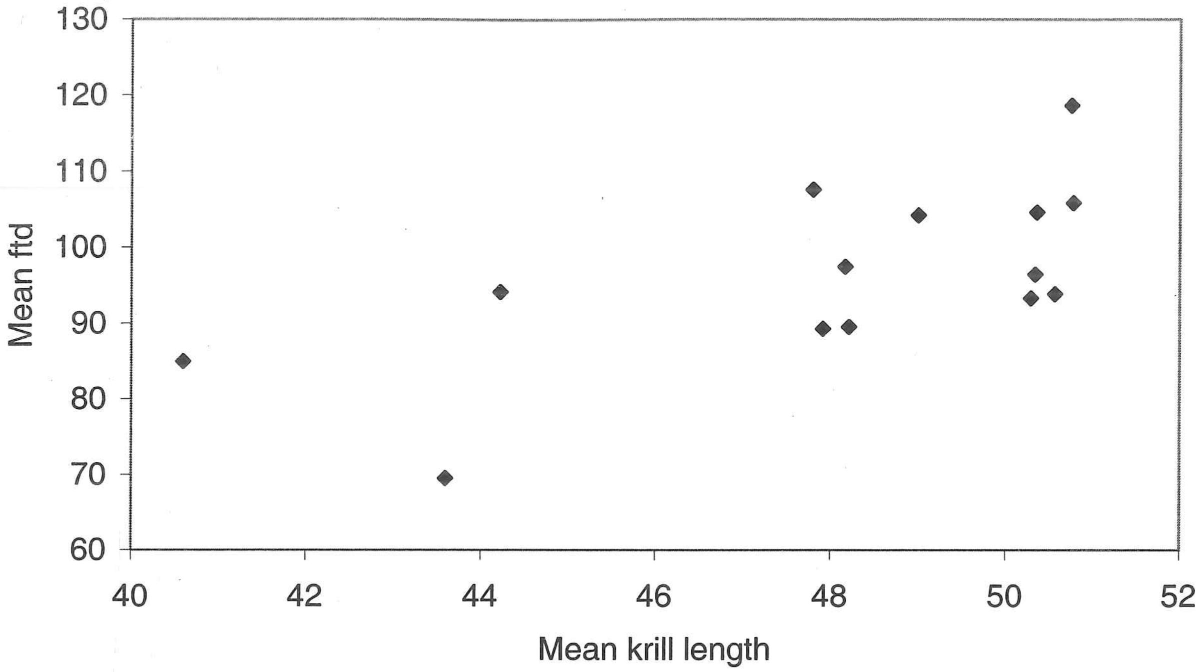

Figure 11: Correlation between mean foraging trip duration and mean krill length for time periods 3-5, 1996 - 2001

4. DISCUSSION

4.1 Summary of Results

The high level of variability in both foraging trip duration and krill population structure is consistent with the highly dynamic marine environment in which female fur seals forage. The extent to which there is a significant relationship between the population structure of krill and the duration of foraging trips does indicate that the abundance of krill was greater when there was a greater proportion of small krill in the population. Thus the positive relationship between krill size and foraging trip duration suggests that longer trips, reflecting lower krill availability, are associated with a greater mean size of krill. This is consistent with the findings of Reid et al. (1999) in which it is suggested that the dominance of large krill is likely to be associated with low krill abundance. This suggests that, although the mass of krill increases as a cubic function of length, the proportion of small krill is the dominant factor driving the changes in abundance. Again this is consistent with the current views on the krill population at South Georgia, where there are relatively rapid growth rates in the species and a high rate of mortality. As a result, there may be a relatively small change in mass of krill from year to year but a considerable (perhaps as much as 70 %) reduction in numbers (Murphy and Reid 2001, Reid et al. in press).

4.2 Limitations within the methods

While the results of the current study are consistent with the present views of krill behaviour at South Georgia, it is clear that there are limitations to linking the concurrent changes in krill population structure to changes in abundance as measured by the foraging trip duration of fur seals. The sampling resolution obtainable using foraging trip duration, for example, is far from ideal, and frequently only very large changes can be detected, as was the case in 1998. It may well be that smaller-scale changes are simply lost in the stochastic 'noise' of the system. It is therefore important to evaluate the potential processes that might produce changes in both the foraging trip duration and krill population structure and abundance. It is equally important to examine the interactions between these processes to determine the extent to which fur seals can be reliably used as samplers of the ecosystem.

Where there is a process that exerts a consistent intra-annual signal, like the increase in foraging trip duration, it is important to take account of such patterns when making comparisons with the length of krill taken through the year. Broadly speaking, the factors influencing foraging trip duration may be divided into two groups: constraints imposed by the seal, and those imposed by the environment. The potential impact of these two forces will be considered further in the following section.

4.3 Intra-annual changes

It is entirely plausible, indeed even quite likely, that as the pup grows the female will spend longer at sea since the energy requirements of the pup will increase, and the period that the pup can survive between meals will also increase. Changes in the time spent foraging in response to the condition of the pup allow the female to optimise her time-energy budget over the course of the lactation period and to maximise the energy delivered to the pup (Boyd 2002). It would be inappropriate to maintain a constant level of provisioning throughout the season, since this would result in a young (small) pup being overfed while an older (larger) pup would be under fed. However, the potential for changes in the composition of the milk during the course of lactation to change the rate of energy delivery without a change in feeding frequency should also be considered (Arnould et al 1995).

The increase in foraging trip duration during the course of lactation strongly suggests that, while the same population structure and abundance of krill might exist at the beginning and end of lactation, the foraging trip duration would differ regardless. Attempts to detect relative changes in krill abundance must thus first take account of any innate increases in foraging trip duration that derive from the maximisation of time-energy budgets during lactation.

The natural mortality of krill during the summer might also have an effect upon changes within krill abundance over the course of the lactation period. The seasonal growth of krill means that the biomass is likely to increase dramatically during the spring growing season. The latter part of the summer however - a time when many krill-dependent species are rearing their offspring - is likely to be a period of high krill mortality with consequent effect upon the abundance of krill. It is unclear whether such a decline in abundance would affect the ability of seals to locate sufficient krill. Nevertheless it is entirely plausible that the increase in foraging trip duration during the course of the summer could reflect an increase in the time taken to locate suitable krill swarms.

4.4 Inter-annual changes

Conspicuously the krill length data are less consistent both within and between years than are the foraging trip duration data. Changes from one year to the next, however, follow a sequential progression associated with episodic recruitment events. Thus in 1996 there was clearly a good recruitment of small krill, which subsequently grew into 1997. There appear to have been few no krill entering the system in 1997 a point illustrated by the absence of smaller krill from the samples taken that year. At the beginning of 1998, only large krill are present, with the gradual appearance of small krill through the summer. The sizes of krill in 1999 seem very large - again suggesting little or no recruitment. In 2000 there was an early recruitment, with the mean size much smaller than in 1999, and in 2001 the mean size increased, reflecting growth of krill and relatively little recruitment.

Thus, 1996 and 2000 were characterised by relatively good recruitment, compared to 1997, 1999 and 2001 where the larger mean size suggests relatively lower levels of recruitment. 1998 is clearly anomalous with the recruitment of small krill not occurring until mid-way through the summer.

In comparing the foraging trip duration and krill it appears that the patterns in 1996 and 2000 were relatively similar with an increase in foraging trip duration over the course of the summer. 1997, 1998 and 2001, by contrast, all showed initial periods of relatively little change, with a sharp increase during the latter part of the year. 1998 was the only year in which foraging trip duration decreased in the latter part of the year – a pattern consistent with a distinct increase in the population of small krill.

4.5 Limitations and further study

This study has provided a preliminary investigation into the causes of change in Antarctic fur seal foraging patterns and has shown links between krill population structure and foraging trip duration. A number of closely intertwined variables, and a lack of knowledge about them mean that the specific effects of different factors are often difficult to identify. More could be understood about the specific causes of change in the foraging trip duration if one or more influences could be factored out in order to observe the effects of just one variable. The variables may be so interdependent that this could be an impossible task, particularly when attempting to determine the cause of minor fluctuations.

Considering the available data, the same relationships could be investigated in more depth if the variation as a component of time could be removed. This would facilitate the identification of patterns, particularly between the foraging trip duration and the proportions of juvenile krill within the year, which credit further investigation. It would also be beneficial to match the krill length data from scat samples with ship based echolocation biomass estimates and net hauled samples. This could corroborate the current thoughts on increasing biomass with decreasing krill length and further explain patterns in the foraging trip duration. However, if data were to be re-collected it may be worth considering a more serial examination at a finer scale. For example if data for each individual were available, a better understanding of the problems facing the seal could be established and the data more easily manipulated in detecting factors such as the cost of pup rearing. Obviously, the more data collected about krill distribution, life cycle and abundance, the easier it would be to detect relationships between variation in krill and foraging trip duration. The need to understand inherent krill biomass could be fulfilled using a fixed mooring with Acoustic Determination of Prey (ADP); this would enable the krill biomass in a particular area to be monitored over a continuous period of time. Coupling this with Fur seal satellite tracking, a clearer picture of their foraging habits and their relation to krill could be seen.

There is still a crucial gap in understanding how the physical environment influences the distribution and abundance of krill (Croxall 1992). The factors affecting the timing of krill recruitment events are unknown. Although investigations of whale feeding patterns has suggested a link between krill abundance and water temperature, the link between the timing of krill recruitment and temperature is essentially unknown (Reid *et al* 2000). Equally, there is relatively limited information on the different spatial characteristics associated with changes in krill abundance. Whether an increase in krill biomass is associated with an increase in the number of swarms has important implications for krill dependant predators.

CONCLUSION

The highly dynamic marine environment creates sampling difficulties if the processes within it are to be measured at appropriate scales. The use of marine predators as samplers of this environment would reduce the logistical complications and results in the collation of a long-term data set. This study has shown large-scale changes in the krill population around South Georgia are easily detected in the foraging trip duration of the female Antarctic fur seals of Bird Island. However small scale changes remain undetected and may simply be lost in the stochastic 'noise' of the system. This should be taken into consideration for future study, as it is important to evaluate potential processes producing change in the factors being assessed, and examine the interactions between them so seals can be used reliably as samples of the ecosystem.

The positive correlation found between foraging trip duration and krill length suggests that longer trips, reflecting lower krill availability, are associated with a greater mean size of krill. The fact that this relationship has been seen without factoring out other influences affecting the two variables of interest, in this highly dynamic environment, is a clear indication that the results of this study can confirm the suggestions made in previous ones, as well as supporting the use of female Antarctic fur seals as samplers of the marine environment.

The further investigation of this topic is essential as detecting and understanding the causes and consequences of long-term change in marine ecosystems are fundamental to many global concerns, not least to successful management of marine resources.

AKNOWLEDGMENTS

The project would not have been possible with out the data provided by the British Antarctic Survey and I am grateful to all involved in its collection. Throughout the project Dr Keith Reid gave support and advice on all aspects of this study also providing much needed directions and corrections. Dr Andy Merrills, Matthew Swarbrick and Liesbeth Renders provided useful suggestions and corrections for the final draft and kept me amused throughout its compilation. Thanks must also go to Dr Colin Harris who enabled the project to be set up and provided much of the preliminary support, and to Dr Akinori Takahashi who provoked thoughtful data analysis. Finally thank you to all those, named and un-named who helped throughout the duration of the dissertation

REFERENCES

Arnould, J.P.Y. and I.L. Boyd, *Temporal Patterns of Milk-Production in Antarctic Fur Seals (Arctocephalus-Gazella).* Journal of Zoology, 1995. 237: p. 1-12.

Arnould, J.P.Y., et al., *Variation in maternal provisioning by lactating Antarctic fur seals (Arctocephalus gazella): response to experimental manipulation in pup demand.* Behavioral Ecology and Sociobiology, 2001. 50(5): p. 461-466.

Atkinson A, M J Whitehouse, J Priddle, G C Cripps, P Ward and M A Brandon *South Georgia, Antarctica: a productive, cold water, pelagic ecosystem* Marine Ecology Progress Series 2001 216: p279-308

Bergstrom B I, G Hempel, H P Marschall, A North, V Siegal and J O Stromberg Spring distribution, size composition and behaviour of krill *Euphausia superba in the western Weddell Sea.* Polar Record 1989 26(157): p85-89

Bonner N *Seals and Sea Lions of the World* Blandford Books 1994

Boyd, I.L. *Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins.* Journal of Applied Ecology 2002, 39, 103-119.

Boyd, I.L. *Foraging and provisioning in Antarctic fur seals: inter-annual variability in time-energy budgets.* Behavioural Ecology, 199910, 198-208.

Boyd, I L *Pup production and distribution of breeding Antarctic fur seals (Arctocephalus gazella) at South Georgia.* Antarctic Science 1993 5: p17-24

Brierley A S, J L Watkins and A W A Murray *international variability in krill abundance at South Georgia.* Marine Ecology Progress Series 1997 150: p87-98

Costa, D.P. and P.A. Prince, *Foraging Energetics of Grey-Headed Albatrosses Diomedea chrysostoma at Bird Island, South Georgia.* Ibis, 1987. 129(2): p. 149-158.

Croxall, J.P. and M.N. Pilcher, *Characteristics of Krill Euphausia superba Eaten by Antarctic Fur Seals Arctocephalus gazella at South-Georgia.* British Antarctic Survey Bulletin, 1984 (63): p. 117-125.

Croxall, J.P., *Southern Ocean environmental changes: effects on seabird, seal and whale populations.* Philosophical Transactions of the Royal Society of London, 1992. Series B(338): p. 319-328.

Croxall J P, P A Prince and C Rickets *Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. Found in Antarctic Nutrient Cycles and Food webs (eds* w r Sieggfried, PA Condy and R M Laws). Spring-Verlag Berlin Heidelberg p516-533

Doidge, D.W., T.S. McCann, and J.P. Croxall, *Attendance behavior of Antarctic Fur Seals,* in Fur Seals: Maternal Strategies on Land and at Sea. Princeton University Press 1986. p. 103-114.

Doidge, D.W. and J.P. Croxall, *Factors affecting weaning weight in Antarctic fur seals Arctocephalus gazella at South Georgia.* Polar Biology, 1989. 9(3): p. 155-160.

Everson I *Krill Biology, Ecology and Fisheries* Blackwell Science Ltd. 2000

Gentry R L and G L Kooyman *Fur Seals: Maternal Strategies on Land and at Sea.* Princeton University Press 1986. p. 103-114.

Headland R *The Island of South Georgia* Cambridge University Press 1984

Knox G A *The Biology of the Southern Ocean* Cambridge University Press 1994

Laws R M *Antarctic Seals Research Methods and Techniques* Cambridge University Press 1993

McCafferty D J, I L Boyd, T R Walker and RI Taylor *Foraging responses of Antarctic fur seals to changes in the marine environment* Marine Ecology Progress Series 1998 166: 285-299

McCann, T.S. and D.W. Doidge, *Antarctic fur Seal, Arctocephalus gazella*, in Status, biology, and ecology of fur seals; Proceedings of an international symposium and workshop, J.P. Croxall and R.L. Gentry, Editors. 1987, NOAA Tech REP NMFS 51: Cambridge. p. 5-8

Murphy, E.J. and K. Reid, *Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem.* Marine Ecology-Progress Series, 2001. 217: p. 175-189.

Nicol S and W de la Mare *Ecosystem management and the Antarctic krill.* American Scientist 1993 81:36-47

Payne, M.R., *Fur seals Arctocephalus tropicalis and A.gazella crossing the Antarctic Convergence at South Georgia.* Mammalia, 1979. 43(1): p. 93-98.

Payne, M.R., *Growth in the Antarctic fur seal Arctocephalus gazella.* J.Zool.,London, 1979. 187: p. 1-20.

Reid, K. and J.P.Y. Arnould, *The diet of Antarctic fur seals Arctocephalus gazella during the breeding season at South Georgia.* Polar Biology, 1996. 16(2): p. 105-114.

Reid, K., et al., *Krill caught by predators and nets: Differences between species and techniques.* Marine Ecology-Progress Series, 1996. 140(1-3): p. 13-20.

Reid, K., et al., *Predicting changes in the Antarctic krill, Euphausia superba, population at South Georgia.* Marine Biology, 1999. 135(4): p. 647-652.
Reid, K., et al., *Krill population dynamics at South Georgia 1991-1997, based on data from predators and nets.* Marine Ecology-Progress Series, 1999. 177: p. 103-114.

Reid, K., *Growth of Antarctic krill Euphausia superba at South Georgia.* Marine Biology, 2001. 138(1): p. 57-62.

Reid, K. and J.P. Croxall, *Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem.* Proceedings of the Royal Society of London Series B-Biological Sciences, 2001. 268(1465): p. 377-384.

Watkins J L, A W A Murray and H I Daly *Variation in the distribution of Antarctic krill Euphausia superba around South Georgia.* Marine Ecology Progress Series 1999 188: 149-160

Watkins J L, F Buchholz, J Priddle, D J Morris and C Ricketts *Variation in reproductive status of Antarctic Krill swarm; evidence for a size-related sorting mechanism?* Marine Ecology Progress Series 1992 82: p163-174